Title: Social complexity and kinship in animal societies

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Abstract

Studies of eusocial invertebrates regard complex societies as those where there is a clear division of labour and extensive cooperation between breeders and helpers, while studies of social behaviour in mammals regard complex societies as those where individual differences in dominance rank and coalitionary support determine access to resources and reproductive opportunities. We show here that traits associated with the complexity of social organisation among females occur in social mammals that live in groups composed of close relatives while traits associated with the complexity of social relationships occur where average kinship between female group members is low. These differences in the form of social complexity appear associated with variation in brain size and may reflect contrasts in the extent of conflicts of interest between group members. Our results emphasize the limitations of any unitary concept of social complexity and highlight that variation in kinship has far-reaching consequences for social behaviour.

Introduction

Although the emergence of complex societies has been identified as one of the major transitions in evolutionary biology (Maynard Smith & Szathmary 1997), what is meant by social complexity is frequently unclear and concepts of complexity vary. Studies of eusocial insects and cooperative vertebrates have mostly followed Wilson (1971) in characterising complex societies as those where there is reproductive suppression of females, extensive alloparental care and a division of labour among females which is often combined with functional divergence in development between breeders and non-breeding workers or between different categories of workers (Bourke & Franks 1995; Anderson & McShea 2001; Abbot & Chapman 2017; Korb & Thorne 2017). In contrast, studies of social mammals (and of the higher primates and cetaceans in particular) regard the presence of frequent competitive interactions, linear dominance hierarchies, reciprocal cooperation, differentiated social relationships, and coalitions and alliances between group members as indicators of social complexity (Byrne & Whitn 1988; Freeberg et al. 2012; Bergman & Beehner 2015; Silk & Kappeler 2017).

There are theoretical grounds for expecting that reproductive suppression, extensive alloparental care by non-breeding females and a division of labour between breeders and non-breeders (which we refer to as 'organisational complexity') are likely to be most highly developed where kinship between group members is high, indirect fitness benefits are substantial and conflicts of interest between group members are reduced (Hamilton 1971; Silk 2002; Boomsma 2009) and comparative studies of insects (Hughes et al. 2008) and birds (Cornwallis et al. 2010) have shown that this is the case. In contrast, conflicts of interest between group members and social traits associated with them, including frequent aggression between group members, well defined

dominance hierarchies and behavioural tactics used to maintain social status (which we refer to as 'relational complexity'), might be expected to be most highly developed in species where most group members are not closely related (Seyfath & Cheney 2012) and conflicts of interest between group members are common. Such differences in the complexity of the social environment may have implications for the development of cognitive abilities and brain structure. Where traits associated with organisational complexity are well developed and there is a clear division of labour between group members that is associated with contrasts in development, social relationships between individuals seldom appear to be as relationships as differentiated or as variable as in species where *relational* complexity is high and individuals frequently need to make decisions that are cognitively demanding (Anderson & McShea 2001).

Social mammals provide an unusual opportunity to explore the relationship between contrasts in the occurrence of these two forms of social complexity and variation in kinship between group members across species since they include both litter-bearing monogamous species, like the social mole rats and some social mongooses, where average coefficients of kinship between female group members are usually between 0.25 and 0.5) as well as species with polygynous or polygynandrous mating systems that bear single offspring, like the smaller cetaceans and all three African apes, where average kinship among female group members seldom exceeds 0.05 (*see Supplementary Table 1*). Moreover, the social behaviour of a relatively high proportion of mammals has been studied in some detail (Clutton-Brock 2016). Here, we use information on variation in social behaviour and kinship structures among mammals to investigate how particular components of *structural* and *relational* complexity are associated with variation in kinship.

Materials and Methods

The objective of our study is to assess whether traits associated with organizational complexity more frequently occur in in social mammals in which average levels of kinship among female group members are high, whereas traits associated with relational social complexity are more likely to be present when average levels of kinship among female group members are low. We extracted information from the published literature and used a phylogenetic comparative approach to assess the association between average levels of kinship observed within social groups and the various behavioural traits. We provide extended details on the methods and definitions of the variables in the Supplementary Materials at the end of this file. All data, and the references we used to obtain them, are provided in Supplementary Table 1.

Average kinship among female group members in mammals

We searched for all populations of social mammals for which average kinship among a group of all adult female individuals had been calculated based on similarity at genetic markers. We started with species included in relevant reviews (Lukas et al. 2005; Briga et al. 2012) and references citing these, and searched for additional studies on Google Scholar (up until August 2017) using the key terms (i) “microsatellite”, (ii) “relatedness” or “kinship”, and (iii) “mammal*”. Studies were included if they provided data on average levels of kinship among all adult female group members based on genetic methods that could be used to estimate the extent of allele sharing at microsatellite loci. We only included species in which females lived in groups where the same individuals repeatedly interact with each other across extended periods: these include cooperative breeders, like meerkats or wolves, in which non-breeding subordinates live with dominant breeders; species where

individuals live in stable groups including multiple breeding females, like many of the social primates; and species where adult females form regular associations by also aggregate in larger, less stable groups, as in red deer or elephants.

Social parameters in mammals

For all the mammalian species for which we were able to find data on average kinship among all adult female group members, we searched the primary literature for information on the occurrence of asymmetrical allomaternal provisioning, infanticide by females, reproductive suppression of subordinate females, division of labour between breeders and nonbreeders, linear dominance hierarchies among group females, and coalition formation in conflicts among females. In addition, we searched for data on rates of aggression between group females and symmetry in grooming interactions. For details see the Supplementary Materials.

Brain and body size

Data on body, brain, and neocortex size were extracted from the published literature (Shultz & Dunbar 2010; Barton & Capellini 2011; Isler & van Schaik 2012). When information was present in several datasets, we calculated median values for species and manually checked for outliers. Since it is still debated exactly how brain size evolves, we relied on four different approaches: first, we used absolute brain size as a response variable in a regression with relational complexity and in a regression with average levels of kinship; second, we used absolute brain size as a response variable in a regression with relational complexity/average kinship while controlling for body size; third, we additionally included longevity, diet, and seasonal variation as predictor variables, ecological parameters which have been indicated to influence brain size variation in mammals; and fourth, we used the size of the neocortex as a response

variable in a regression with relational complexity and in a regression with average levels of kinship. We used comparative databases to extract information on diet category and activity strata (de Magalhaes & Costa 2009; Jones et al. 2009; Price et al. 2012; Botero et al. 2014; Wilman et al. 2014).

Statistical approaches

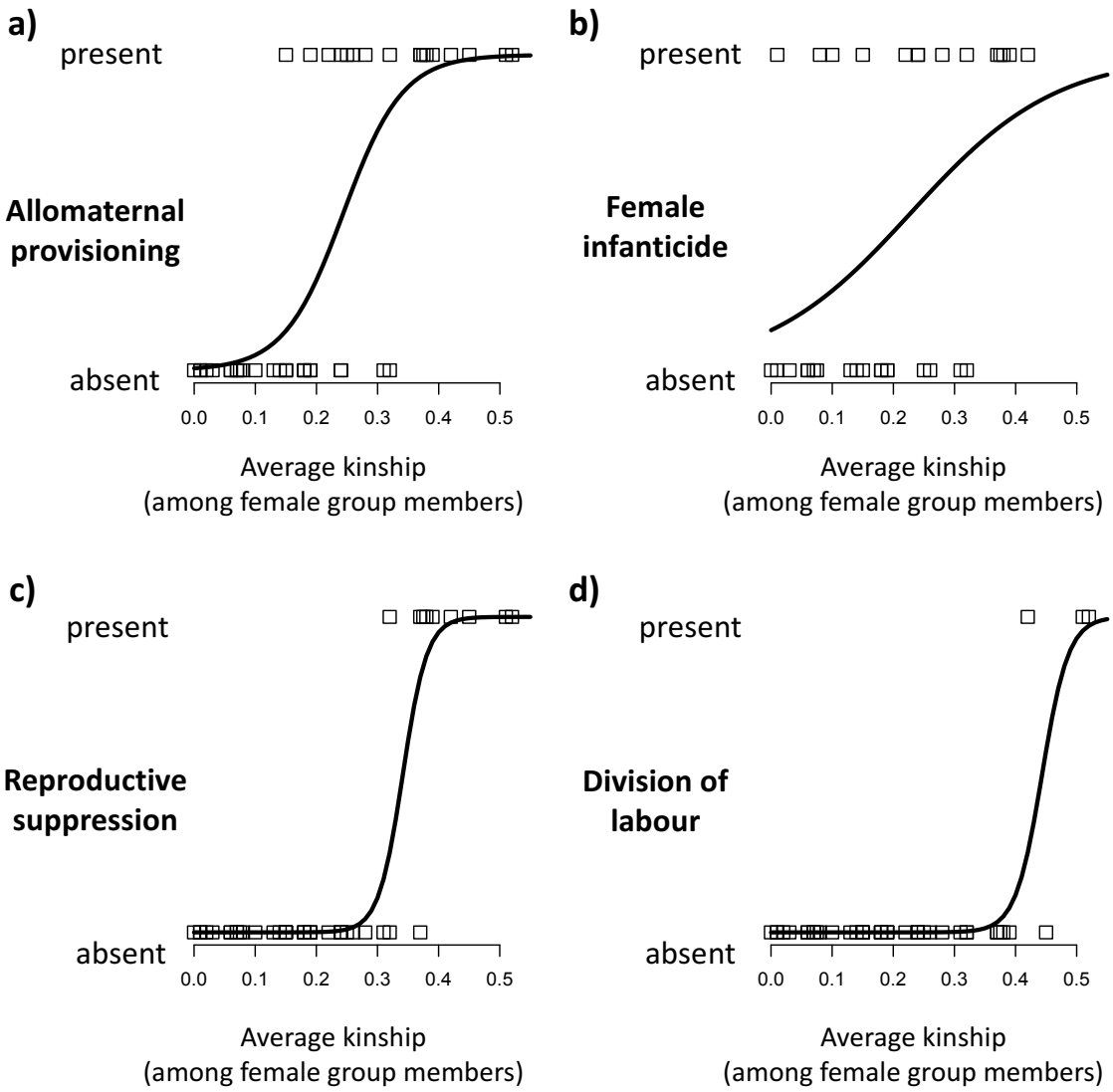
Regressions to assess the relationship across mammals between specific forms of behaviour and average levels of kinship were performed while accounting for phylogenetic relatedness among species using MCMCglmm (Hadfield & Nakagawa 2010). We relied on the updated mammalian supertree (Fritz et al. 2009) to estimate phylogenetic relatedness between species. The tree was truncated to match our sample using functions of the package 'ape' (Paradis et al. 2004) in the statistical software R (R Development Core Team 2010). We included the phylogenetic relationship between species as covariance matrix, used a broad prior, 1,000,000 iterations, a burn-in of 200,000, and a thinning interval of 10. The analysis was repeated three times, and visually inspected for convergence. Terms were considered statistically significant when the calculated pMCMC values were less than 0.05.

Results

As among insects (Hughes et al. 2008) and birds (Cornwallis et al. 2010), traits associated with organisational complexity (including the presence of non-breeding female helpers, extensive provisioning of juveniles by females other than the mother and a clear division of labour between breeders and non-breeders) are more commonly found in social mammals where average levels of kinship between females living in the same group are high than where they are low (Fig 1, a-d: effect of average kinship on presence of: *allomaternal provisioning* 117.32 (95% CI 16.2, 227.7), $p<0.001$, n=41 species; *female infanticide* 139.4 (95%CI -4.4, 409.2), $p=0.03$, n=31 species; *reproductive suppression* 276.9 (95%CI 57.7, 441.3), $p<0.001$, n=42 species; *division of labour* 216.2 (95% CI 41.3, 325.5), $p<0.001$; all n=42 species). In some species where average kinship between group members is high and traits associated with organisational complexity are present (including naked molerats and Kalahari meerkats), there are also obvious morphological differences between breeding and non-breeding females which resemble those between queens and workers in eusocial insects, though they are less pronounced (Bennett & Faulkes 2000; Clutton-Brock 2016; Zöttl et al. 2016). While helpers are usually closely related to the young they are raising in these species, individual differences in contributions to alloparental care are seldom closely associated with variation in relatedness between helpers and the individuals that they are assisting (Griffin & West 2003; Clutton-Brock 2006).

Fig 1. Average levels of kinship among female group members and occurrence of traits associated with organisational complexity across social mammals

Traits associated with high organisational complexity - extensive provisioning by females other than the mother (a), female infanticide (b), suppression of reproduction in subordinate females (c), and a well-defined division of labour between breeding females and helpers (d) – are all more frequently present in species with high average levels of kinship between group members than in those where average kinship between group members is low.



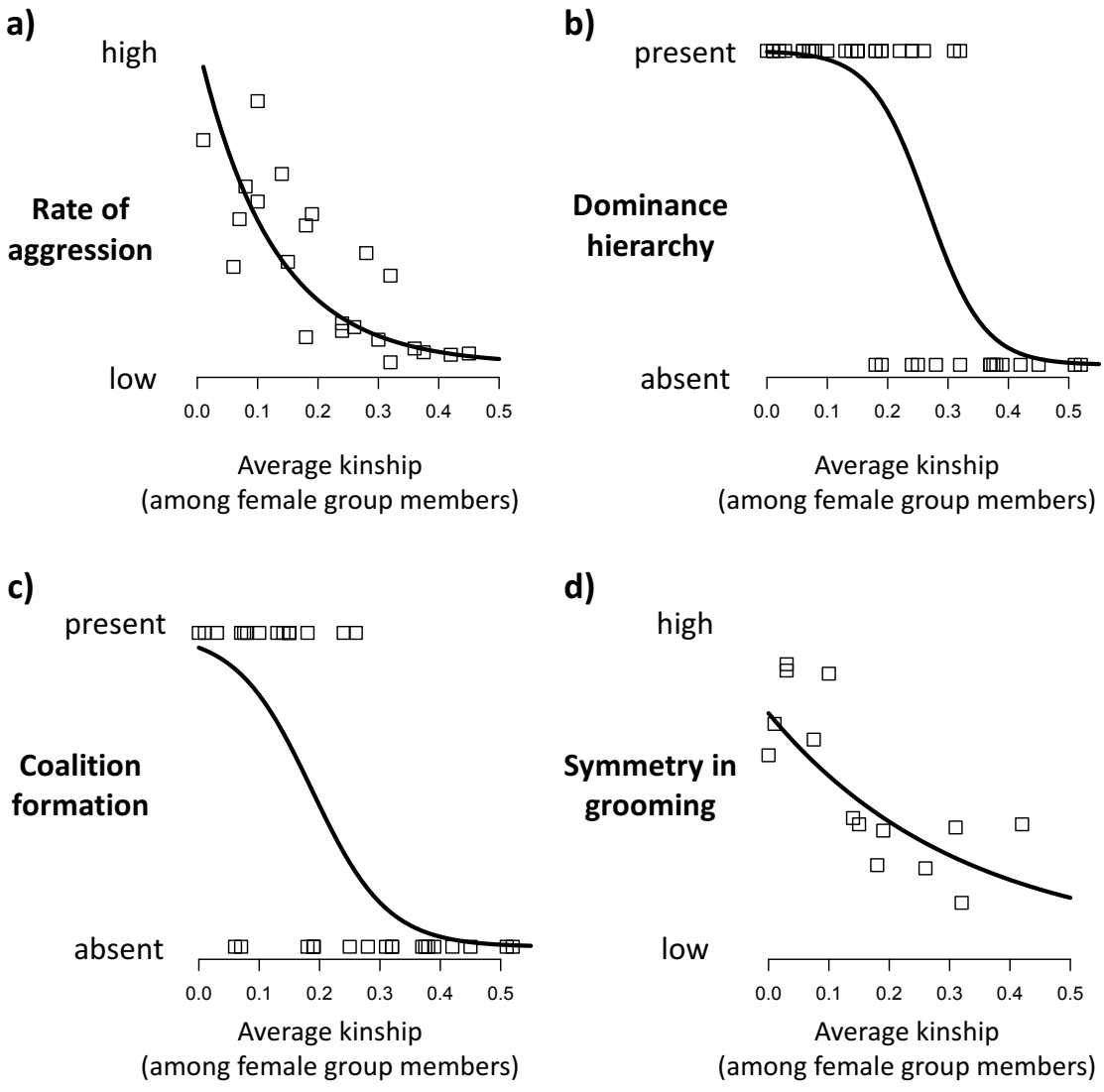
In contrast, high rates of aggression between females, well defined linear dominance hierarchies and differentiated social relationships between individuals involving coalitions and alliances are typically found in species where average kinship between group members is low. The frequency of aggressive interactions between female group members increases as average kinship between resident females falls (Fig 2a: effect of average kinship on *rate of aggression per female per hour* -4.0 (95%CI -7.5, -0.6), p=0.03; n=22 species) and average kinship between females is a better predictor of rates of aggression between individuals than the number of adult group members (effect of average kinship on *rate of aggression per female per hour* -2.5 (95% CI -5.31, -1.62), p=0.01, effect of number of adult females per group 0.03 (95% CI -0.02, 0.08), p=0.32; n=22 species). Contrary to some predictions (Isbell 1991; Sterck et al. 1997), interspecific differences in rates of aggression among females do not appear to be closely associated with major species differences in diet, habitat use or longevity among the species in our data set (*Supplementary Table 2*). Well defined dominance hierarchies that include all resident females are also more commonly found where average kinship between group members is low than where they are high (Fig 2b: effect of average kinship on *presence of linear dominance hierarchy* –198.9 (95%CI -429.8, -17.6), p<0.01; n=42 species) although there is commonly a clear difference in dominance between breeding females and non-breeding helpers in groups where both are present. Supportive coalitions between female group members (which are often used in competition for resources or breeding partners) are also more frequent in species where average kinship between group members is low (Fig 2c: effect of average kinship on *presence of coalitionary behaviour* -261.1 (95% CI -445.2, -57.1), p<0.001; n=42 species) and are usually rare or absent in species where average kinship between group members is high and groups include nonbreeding helpers. Several other behavioural traits, including the redirection of aggression, reconciliation

and consolation between female group members (Byrne & Whiten 1988; Marino et al. 2007; Jaeggi & Gurven 2013) also appear to be restricted to species living in groups where kinship between group members is low, although the available data do not yet allow quantitative comparisons.

Contrasts in average kinship between group members may also affect the distribution of cooperative behaviour between interacting individuals: in species where few group members are close relatives, individuals commonly direct asymmetrical forms of assistance at the relatively small number of individuals to which they are closely related (Silk 2002) whereas, in species where most group members are close relatives, there is usually little evidence that closer kin are preferentially targeted (Griffin & West 2003, Clutton-Brock 2006). Mutualistic forms of cooperation, like social grooming, can occur whether group members are closely related or not but, since individuals are unlikely to gain substantial indirect fitness benefits where levels of kinship between group members are low, interactions should be more symmetrical in species where cooperating partners are not closely related (Lehmann & Keller 2006). In line with this prediction, allogrooming relationships appear to be more symmetrical in species where average kinship between group members is low than where it is high (Fig 2d: effect of average kinship on *reciprocity in pairwise grooming interactions* -1.4 (95%CI -2.36, -0.43), $p<0.01$; n=13 species).

Fig 2. Average levels of kinship among female group members and occurrence of traits associated with relational complexity across social mammals

Traits associated with high *relational* complexity – (a) frequent aggressive interactions among group members (rate of aggression between female group members), (b) well-defined linear dominance hierarchies, (c) coalition formation in fights among group members, and (d) symmetry in cooperative interactions (reciprocity in grooming interactions among female group members) – are all more likely to be present in species with low average levels of kinship between group members than in those where average kinship between group members is high.



It has been suggested that complex, social relationships between group members may have favoured the evolution of improved cognitive abilities and increases in brain development (Dunbar & Shultz 2007), though the extent to which gross differences in relative brain size reflect contrasts in in cognitive abilities has been questioned (Logan et al. 2017) and the relative effects of social versus ecological parameters on brain development are widely debated (Clutton-Brock & Harvey 1980; Isler & van Schaik 2014; deCasien et al. 2017). Previous studies have shown that eusocial insects (Farris 2016) and cooperatively breeding birds (Iwaniuk & Arnold 2004) frequently have brain sizes smaller than related non-cooperative taxa while, in mammals, several cooperative breeders show little evidence of advanced cognitive abilities (Thornton & McAuliffe 2015). In contrast, many of the mammals that are thought to possess the most advanced cognitive abilities have relatively large brains (like the higher primates, the social hyenas and the smaller cetaceans) and live in groups where average kinship between group members is low and social relationships between individuals are complex and unstable (Marino et al. 2007; Clutton-Brock 2016). Across the mammals in our sample, indices of both absolute and relative brain size are positively associated with the expression of traits associated with *relational* complexity (effect of presence of traits associated with relational complexity on log-transformed *brain mass* 1.84 (95% CI 0.7, 2.9), $p = 0.001$, $n = 36$ species) and negatively with estimates of average kinship between female group members (effect of average kinship among females on log-transformed *brain mass* -6.1 (95% CI -9.79, -2.75), $p<0.01$, $n=36$ species). Both these associations are present after accounting for the effects of body size, diet, and arboreality on variation in brain size and persist when estimates of relative brain size are replaced by other estimates of brain development, including the size of the neocortex (*Supplementary Table 3*).

Discussion

Our analysis emphasises the limitations of any unitary concept of social complexity: traits associated with a clear division of reproduction and labour between group members are seldom highly developed in species where traits associated with relational complexity are highly developed and vice versa. Moreover, there are other forms of social complexity, including variation in the stability of groups and the frequency with which members of different groups associate with each other (Kummer 1968; Moss & Lee 2011).

Our analyses support Hamilton's (1971) suggestion that variation in kinship is likely to have far-reaching consequences for social behaviour and social relationships among vertebrates as well as among invertebrates (Bourke 1999, Silk 2002). One reason why the association between complex, differentiated social relationships and low average levels of kinship between group members has not been widely recognised may be the assumption that average levels of kinship are high in social animals where females commonly breed in the group where they are born so that most female group members are related to each other. However, even where most females remain in their natal groups throughout their lives, average kinship between resident females is usually low if groups include multiple breeding females, including individuals from successive generations, mating systems are polygynous or polygynandrous, and the breeding tenure of males is short (Lukas et al. 2005). As a result, conflicts of interest between group members are likely to be common and may promote the evolution of traits used in competitive encounters, including competitive coalitions and alliances and complex forms of manipulation (Byrne & Whiten 1988).

Comparisons between species also suggest that cognitive capacities and brain size may be more highly developed in animals social where average kinship between group members is low and social relationships are complex and competitive than in those where average kinship is high and reproductive suppression and cooperation are highly developed as the 'social brain' hypothesis suggests. However, previous studies have shown that the relationship between gross differences in brain size and cognitive abilities is inconsistent and the effects of variation in social behaviour on brain development are disputed (Clutton-Brock & Harvey 1980; Isler & van Schaik 2014; deCasien et al. 2017; Dunbar & Shultz 2017).

The association between average kinship between group members and the two contrasting forms of social complexity may also have implications for our understanding of the evolution of human societies. Most of the higher primates and all three African apes live in social groups where average coefficients of relatedness between group members are low and reproductive suppression of adult females, alloparental provisioning and a division of labour between group members are rare (Lukas & Clutton-Brock 2012). Since hominins presumably developed from ancestors that lived in groups where average kinship between group members was also low (Chapais 2009; Hill et al. 2011), this suggests that the presence of extensive alloparental care and a pronounced division of labour between group members in human and non-human societies is likely to have evolved by different evolutionary pathways.

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Statement of authorship: DL and TCB designed the study; DL collected the data and carried out statistical analyses; DL and TCB wrote the manuscript; and DL and TCB gave final approval for publication.

Data accessibility:

All data are included as supplement and are deposited at the Knowledge Network for Biocomplexity (doi:10.5063/F1FB513K).

Keywords: sociality; evolution; social complexity; eusociality; behaviour; cooperation; competition; kinship; relatedness

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Supplementary Material for pre-peer-reviewed version of:

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Social complexity and kinship in mammal societies

505

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509 **Supplementary text:** Extended methods and definitions of the variables

510 **Table S1:** All data used in the analyses with references

511 **Table S2:** Output of the statistical model assessing the association between rates of

512 aggression among females and ecological parameters

513 **Table S3:** Output of the statistical models assessing the association between

514 measures of brain size and relational complexity and average levels of kinship

515

Supplementary text: Extended methods and definitions of variables

In the following, we provide more information on the definition of the variables and our data collection procedures. This additional information is included here as the article was submitted to a journal with word limits but without copyright transfer of the supplementary material.

Average kinship among female group members in mammals

We searched for all populations of social mammals for which average kinship among a group of all adult female individuals had been calculated based on similarity at genetic markers. We started with species included in relevant reviews (Lukas et al. 2005; Briga et al. 2012) and references citing these and searched for additional studies on Google Scholar (up until August 2017) using the key terms (i) “microsatellite”, (ii) “relatedness” or “kinship”, and (iii) “mammal*”. Studies were included if they provided data on average levels of kinship among all adult female group members based on genetic methods that could be used to estimate the extent of allele sharing at microsatellite loci. We only included species in which females lived in groups where the same individuals repeatedly interact with each other across extended periods. These include cooperative breeders, like meerkats [*Suricatta suricata,* Schreber 1776] or wolves [*Canis lupus,* Linnaeus 1758], in which non-breeding subordinates live with dominant breeders; species where individuals live in stable groups including multiple breeding females, like many of the social primates; and species where adult females form regular associations but also aggregate in larger, less stable groups, as in red deer [*Cervus elaphus,* Linnaeus 1758] or elephants [*Loxodonta Africana,* Blumenbach

542 1797]. Some studies reported levels of kinship among dyads based on the degree of
543 microsatellite allele sharing, relative to the average sharing in the population. Here,
544 estimates were taken directly from the publications based on calculations by the
545 original authors. Average kinship based on these estimates approximates to 0.5 for
546 parent-offspring and full-sibling relations, 0.25 for half-siblings, and 0.00 for individuals
547 distantly or un-related, and can even be negative if individuals share fewer alleles than
548 expected (for example, if individuals are immigrants into the local population). Where
549 average kinship among females was negative, we set this value to 0.00 to match data
550 derived from pedigrees (see next), indicating that individuals are unrelated. For some
551 species, multi-generational pedigrees and data on maternity and genetically-
552 determined paternity were available for all adult individuals, and here, we derived
553 kinship levels for adult females from the pedigree for all same-sex dyads, setting
554 relatedness to 0.5 for parent-offspring or full-siblings, 0.25 for half-siblings (populations
555 did not contain any adults whose grandparents were still alive), and 0.00 for all
556 remaining less closely related pairs. For the species in which we have information both
557 on average relatedness and pedigree relationships, the values from the two methods
558 correlate closely (n=7 species, r^2=0.85, p<0.01), so we treated data from both
559 measures equally. In instances in which multiple estimates of average kinship among
560 females were present (either from multiple social groups within the same study or from
561 different studies), we calculated the average across reported values to generate a
562 single value per species.
563
564 *Social parameters in mammals*
565 For all the mammalian species for which we were able to find data on average kinship
566 among all adult female group members, we searched the primary literature for
567 information on (i) the presence or absence of allomaternal provisioning, (ii) infanticide

by females, (iii) reproductive suppression of subordinate females, (iv) division of labour between breeders and nonbreeders, (v) linear dominance hierarchies among group females, and (vi) coalition formation in conflicts among females. In addition, we searched for quantitative data on (vii) rates of aggression between group females and (viii) symmetry in grooming interactions. We assigned each species a single value for each behaviour. For the first six social parameters, we assumed them to be present if observations had been reported and to be absent if the no reports existed despite direct observations or if papers stated that the parameter is absent. For the latter two social parameters, we extracted quantitative estimates either from single reports or as averages across multiple values, even if values were recorded in different populations or at different times than when levels of kinship had been calculated. For some parameters, data are only available for a small number of species and additional data may alter the relationships we describe. Our aim was to provide a framework for research into social complexity and we hope that it will stimulate further analyses.

Alloparental provisioning

We considered alloparental care to be present if females contribute to the nursing or feeding of offspring that are not their own. We focused on these two provisioning behaviours (compared to behaviour such as group defense) as they can be easily observed, are likely to carry an immediate cost, and are clearly targeted at offspring. We based our classification on the review by Packer et al. (1991) and differentiated between species in which all offspring receive at least some support from females that are not their mothers (alloparental care present) from those in which offspring never receive alloparental support or rare instances most likely represent theft (alloparental care absent).

Female infanticide

We obtained data on the occurrence of female infanticide (the killing of conspecific young by females) from reviews and the primary literature. We only included records of female infanticide from wild populations in which the killer was unambiguously identified as an adult female and females killed neonates born to others in the same group that they lived in. Species recorded as not showing female infanticide were restricted to those where natural observations on breeding females and juveniles were available over more than three reproductive seasons and female infanticide was not reported. Since in most species records of female infanticide originate during ad libitum observations rather than systematic observations, we did not calculate rates of offspring mortality from infanticide, but only scored whether instances of females killing offspring born to other mothers had been observed (infanticide present) or not (infanticide absent).

Reproductive suppression of subordinate females

Groups were classified as containing non-breeding adults if records showed that more than half of all subordinate females in a group did not breed successfully in a single breeding season. Levels of reproductive skew among females within social groups are not continuously distributed across mammals, but clearly fall into two categories of either high or low skew (Lukas & Clutton-Brock 2012, Rubenstein et al. 2016), supporting a binary classification into those species in which non-breeding females are present versus those in which they are absent. Non-reproductive female group members do not necessarily participate in social activities and might simply be tolerated by dominant breeders (see also Griesser et al. 2017).

Reproductive division of labour between breeders and nonbreeders

We followed Wilson (1971) in classifying species as having a reproductive division of labour if non-breeders show contributions to the care of young born to breeders that consistently differ from the maternal care shown by breeders. Activities that, in these species, are only shown by non-breeders include babysitting, digging for food, carrying offspring, or feeding weaned offspring. A reproductive division of labour can only occur in species in which non-reproducing females and alloparental care are present (the two variables defined above) but is only present in a subset of these species. We decided to include these separate categories as they might facilitate comparisons with other taxonomic groups. In addition, we would predict that they represent increases in organisational complexity, and that the association between high levels of average kinship among group members and a reproductive division of labour is particularly pronounced.

Dominance hierarchies

We classified groups as having linear dominance hierarchies if studies showed that all female group members could be arranged in a linear ordering based on their aggressive/submissive interactions. If interactions among some individuals were too rare to determine their relative status, species were classified as not having dominance hierarchies, even if they contained a single individual who was clearly dominant. For the subset of species in which linear dominance hierarchies were reported to be present among females, we searched for data on the stability of the hierarchy as measured by Vries' (1998) linearity index *h′*, which ranges from 0 (in situations where all individuals are equally likely to win during an aggressive encounter) to 1 (in situations where all dyadic relationships are fully decided and relationship among all individuals are transitive).

646 *Within-group coalitions*

647 We based our data on the occurrence of coalitions between individuals on relevant
648 reviews (Olson & Blumstein 2009; Bissonnette et al. 2015), and checked papers
649 referenced in or citing these reviews. We recorded coalitionary support during
650 aggressive interaction as occurring if some interactions between females belonging to
651 the same social groups involved two females simultaneously threatening or attacking
652 one or more other same-sex individuals from the same group. We excluded species in
653 which individuals only formed coalitions against individuals from other groups.

654

655 *Rates of aggression*

656 We collected data on rates of aggression between female group members in wild
657 populations from relevant reviews (Fournier & Festa-Bianchet 1995; Wheeler et al.
658 2013), and we searched for primary publications reporting observations of aggression
659 in species for which we had data on average kinship. We recorded the number of any
660 form of aggressive interactions per individual per hour involving other group members
661 of the same sex. We excluded studies in which authors had only recorded high-
662 intensity aggression as well as studies of captive animals. Since rates of interactions
663 are influenced by how often dyads are in physical proximity or not, we only included
664 species in which social groups are stable and coherent, excluding species where
665 individuals form fission/fusion groups, like chimpanzees or dolphins, as well as those
666 where groups are unstable and individuals are often widely dispersed, as in many
667 ungulates and macropods.

668

669 *Grooming symmetry*

670 We extracted information on the degree of symmetry in grooming interactions between
671 females from studies in which authors reported the correlation in grooming efforts

672 (depending on how it was measured in a given study, i.e. amount time spent grooming
673 or number of bouts) between all pairs of female group members (Schino & Aureli 2008).
674 We extracted reports of the Pearson product moment correlation coefficient between
675 the pairwise matrix showing all grooming given from females to all female partners and
676 the matrix showing all grooming received. A value of -1 indicates a complete mismatch
677 among all pairs, where individuals who receive the most grooming give the least, a
678 value of 0 indicates that grooming is distributed randomly, and a value of +1 indicates
679 that in all dyads individuals perfectly match each other. High symmetry in grooming
680 likely reflects that individuals have differentiated relationships, whereas dyads might
681 show imbalances in grooming if individuals are related and might receive indirect
682 fitness benefits from their efforts. For comparative purposes, we used values reported
683 in a previous meta-analysis (Schino & Aureli 2008) even if additional primary
684 information was available, and added single values for species from analyses which
685 used an identical approach.
686
687 *Combined presence of traits associated with relational complexity*
688 In order to combine the three traits into a single measure as a proxy for the extent to
689 which traits of *relational* complexity are expressed in a given species, we transformed
690 the data on rates of aggression among females into a binary variable, classifying
691 species with rates of aggression above the median (0.745 interactions/female/hour) as
692 having frequent aggression and those with rates below the median as not. We then
693 used this classification of the presence or absence of frequent aggression, the
694 classification on the presence or absence of a dominance hierarchy, and the
695 classification on the presence or absence of coalitionary support to determine the
696 relative presence of traits associated with *relational* complexity. A species in which all
697 of these three traits for which we had data were absent was scored as 0, as 0.33 if one

of the three traits was present, all the way up to 1 if all of the three traits for which we had data were present.

Group size

We obtained data on the number of individuals residing in social groups from papers reporting levels of kinship. For the purpose of this paper, group size was the total number of females of reproductive age, including both breeding and non-breeding individuals. We calculated the average number of females across all social groups for which levels of kinship had been calculated.

Brain and body size

Data on body, brain, and neocortex size were extracted from the published literature (Shultz & Dunbar 2010; Barton & Capellini 2011; Isler & van Schaik 2012). When information was present in several datasets, we calculated median values for species and manually checked for outliers. Since it is still debated exactly how brain size evolves, we relied on four different approaches: first, we used absolute brain size as a response variable in a regression with *relational* complexity and in a regression with average levels of kinship; second, we used absolute brain size as a response variable in a regression with *relational* complexity/average kinship while controlling for body size; third, we additionally included longevity, diet, and seasonal variation as predictor variables, ecological parameters which have been indicated to influence brain size variation in mammals; and fourth, we used the size of the neocortex as a response variable in a regression with *relational* complexity and in a regression with average levels of kinship. We used comparative databases to extract information on diet category, longevity and activity strata (de Magalhaes & Costa 2009; Jones et al. 2009; Price et al. 2012; Botero et al. 2014; Wilman et al. 2014).

724

725 *Statistical Models*

726 We built the following regression models: four models with average levels of kinship
727 as a predictor of each of the traits of *organisational* complexity (alloparental
728 provisioning, female infanticide, reproductive suppression, reproductive division of
729 labour; these traits were coded binary as presence/absence and we assumed a
730 categorical distribution for each of them); five models with average levels of kinship as
731 a predictor of each of the traits associated with *relational* complexity (rates of
732 aggression, reciprocity in grooming, strictness of dominance hierarchy: these traits
733 were coded as continuous measure, assuming a gaussian distribution for them; and
734 linear dominance hierarchy, coalitionary behaviour: these traits were coded binary as
735 presence/absence and we assumed a categorical distribution for them); models with
736 absolute brain mass as the response variable (log10 transformed, coded continuously,
737 assuming a gaussian distribution) and the combined measure of *relational* complexity
738 as predictor variable on its own, the combined measure of *relational* complexity
739 together with body mass, and together with body mass and diet/arboreality; and
740 models with absolute brain mass as the response variable (log10 transformed, coded
741 continuously, assuming a gaussian distribution) and average levels of kinship as
742 predictor variable on its own, average levels of kinship together with body mass, and
743 together with body mass and diet/arboreality.

744

745 **Supplementary Table S1:** Average levels of kinship and traits associated with organisational and with relational complexity across
746 social mammals (references for data are listed in brackets). The table is arranged by average kinship among female group members
747 (from high to low). For a text copy of the dataset see: https://knb.ecoinformatics.org/#view/doi:10.5063/F1FB513K
748

Species	Average kinship among female group members	Number of adult females per group	Alloparental provisioning	Infanticide by females	Reproductive suppression	Reproductive division of labour	Rate of aggression among female group member (acts per female per hour)	Dominance hierarchy among female group members	Reciprocity in grooming among female group members (correlation between grooming given and received across all dyads)	Coalitions among female group members	Presence of relational complexity	Brain Mass (grams)	Neocortex Mass (grams)	Body Mass (grams)	Diet	Strata
Cryptomys damarensis	0.52 (1)	10 (1)	Present (1)	NA	Present (60)	Present (60)	NA	Absent (80)	NA	Absent (80)	0.00	1.80	NA	162.00	Herbivore	Ground
Saguinus mystax	0.51 (1)	2 (1)	Present (1)	NA	Present (60)	Present (60)	NA	Absent (99)	NA	Absent (81)	0.00	11.10	5.88	535.00	Omnivore	Arboreal
Castor canadensis	0.45 (1)	2 (1)	Present (1)	NA	Present (60)	Absent (60)	0.09 (61)	Absent (82)	NA	Absent (82)	0.00	45.90	NA	19286.00	Herbivore	Ground
Suricata suricatta	0.42 (1)	5 (1)	Present (1)	Present (34)	Present (60)	Present (60)	0.08 (62)	Absent (62)	0.39 (91)	Absent (83)	0.00	10.29	NA	776.00	Omnivore	Ground
Canis simensis	0.39 (1)	2 (1)	Present (1)	Present (35)	Present (60)	Absent (60)	NA	Absent (35)	NA	Absent (84)	0.00	80.67	NA	12675.00	Carnivore	Ground
Sus scrofa	0.38 (1)	3 (1)	Present (1)	Present (36)	Present (60)	Absent (60)	NA	Absent (85)	NA	Absent (85)	0.00	180.93	NA	111900.00	Omnivore	Ground
Callithrix jacchus	0.375 (1)	2 (1)	Present (1)	Present (37)	Present (60)	Absent (60)	0.1 (63)	Absent (63)	NA	Absent (81)	0.00	7.37	4.37	342.00	Omnivore	Arboreal
Ctenodactylus gundi	0.37 (1)	3 (1)	Present (1)	NA	Absent (60)	Absent (60)	NA	Absent (86)	NA	Absent (86)	0.00	NA	NA	289.00	Herbivore	Ground

Vulpes vulpes	0.37 (1)	NA	Present (1)	Present (38)	Present (60)	Absent (60)	NA	Absent (100)	NA	NA	0.00	45.21	NA	4897.00	Omnivore	Ground
Helogale parvula	0.36 (2)	4 (2)	NA	NA	NA	NA	0.13 (64)	NA	NA	NA	0.00	NA	NA	NA	NA	NA
Alouatta seniculus	0.32 (4)	3 (4)	Absent (4)	Absent (40)	Absent (60)	Absent (60)	0.02 (65)	Present (4)	NA	Absent (81)	0.33	49.90	31.66	6049.00	Herbivore	Arboreal
Canis lupus	0.32 (1)	2 (1)	Present (1)	Present (41)	Present (60)	Absent (60)	0.71 (66)	Absent (66)	0.14 (92)	Absent (84)	0.00	128.32	NA	30750.00	Carnivore	Ground
Colobus guereza	0.31 (1)	3 (1)	Absent (1)	Absent (40)	Absent (60)	Absent (60)	NA	Present (101)	0.38 (93)	Absent (81)	0.50	76.85	NA	9838.00	Herbivore	Arboreal
Equus burchellii	0.3 (5)	3 (5)	NA	NA	NA	NA	0.2 (67)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Lycaon pictus	0.28 (1)	4 (1)	Present (1)	Present (42)	Absent (60)	Absent (60)	0.89 (68)	Absent (68)	NA	Absent (84)	0.33	129.00	NA	26817.00	Carnivore	Ground
Panthera leo	0.26 (1)	6 (1)	Present (1)	Absent (43)	Absent (60)	Absent (60)	0.3 (69)	Present (69)	0.25 (94)	Present (84)	0.67	231.06	121.09	157250.00	Carnivore	Ground
Octodon degus	0.25 (1)	4 (1)	Present (1)	Absent (44)	Absent (60)	Absent (60)	NA	Absent (87)	NA	Absent (87)	0.00	2.10	NA	235.00	Herbivore	Ground
Eulemur fulvus	0.24 (6)	3 (6)	Absent (30)	Present (45)	Absent (60)	Absent (60)	0.33 (70)	Present (6)	NA	Present (81)	0.67	23.29	12.21	2788.00	Herbivore	Arboreal
Oryctolagus cuniculus	0.24 (1)	3 (1)	Present (1)	Present (46)	Absent (60)	Absent (60)	0.27 (71)	Absent (46)	NA	NA	0.00	10.30	NA	1653.00	Herbivore	Ground
Pecari tajacu	0.24 (1)	NA	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (102)	NA	NA	1.00	101.50	NA	20869.00	Omnivore	Ground
Cuon alpinus	0.22 (1)	NA	Present (1)	Present (47)	Absent (60)	Absent (60)	NA	Present (103)	NA	NA	1.00	94.80	NA	14255.00	Carnivore	Ground
Ctenomys sociabilis	0.19 (7)	2 (7)	Present (29)	NA	Absent (60)	Absent (60)	NA	Absent (88)	NA	Absent (88)	0.00	NA	NA	NA	Herbivore	Ground
Papio hamadryas	0.19 (8)	8 (8)	Absent (31)	Absent (40)	Absent (60)	Absent (60)	1.2 (72)	Present (72)	0.37 (95)	Absent (81)	0.67	145.11	118.78	16014.00	Omnivore	Ground

Propithecus verreauxi	0.19 (9)	3 (9)	Absent (29)	Absent (48)	Absent (60)	Absent (60)	NA	Present (9)	NA	Absent (81)	0.50	26.45	12.19	4329.00	Herbivore	Arboreal
Cebus capucinus	0.18 (1)	7 (1)	Absent (1)	Absent (49)	Absent (60)	Absent (60)	1.11 (73)	Present (104)	0.26 (93)	Present (81)	1.00	71.28	46.43	2629.00	Omnivore	Arboreal
Colobus vellerosus	0.18 (10)	9 (10)	Absent (99)	Absent (50)	Absent (60)	Absent (60)	0.22 (74)	Present (112)	NA	Absent (113)	0.33	NA	NA	NA	NA	NA
Lontra canadensis	0.18 (11)	NA	Absent (11)	NA	Absent (60)	Absent (60)	NA	Absent (11)	NA	NA	0.00	52.31	NA	7808.00	Carnivore	Ground
Cynomys ludovicianus	0.15 (13)	3 (13)	Absent (29)	Present (51)	Absent (60)	Absent (60)	NA	Present (90)	NA	Present (90)	1.00	6.66	NA	958.00	Herbivore	Ground
Loxodonta africana	0.15 (1)	7 (1)	Absent (1)	Absent (52)	Absent (60)	Absent (60)	0.82 (75)	Present (52)	NA	Present (84)	1.00	4789.45	2460.00	4153500.00	Herbivore	Ground
Macaca mulatta	0.15 (14)	NA	Present (29)	NA	Absent (60)	Absent (60)	NA	Present ()	0.39 (93)	Present ()	1.00	NA	NA	NA	NA	NA
Tursiops aduncus	0.15 (1)	8 (1)	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (89)	NA	Present (89)	1.00	NA	NA	NA	NA	Marine
Macaca fascicularis	0.14 (15)	9 (15)	Absent (29)	Absent (40)	Absent (60)	Absent (60)	1.52 (73)	Present (105)	0.41 (93)	Present (81)	1.00	64.51	NA	4909.00	Carnivore	Ground
Varecia variegata	0.13 (16)	3 (16)	Absent (29)	Absent (48)	Absent (60)	Absent (60)	NA	Present (16)	NA	Present (81)	1.00	31.59	NA	3551.00	Herbivore	Arboreal
Antilocapra americana	0.1 (17)	8 (17)	NA	NA	NA	NA	2.1 (76)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Crocuta crocuta	0.1 (18)	14 (18)	Absent (29)	Present (49)	Absent (60)	Absent (60)	1.3 (77)	Present (18)	NA	Present (84)	1.00	149.17	85.20	63000.00	Carnivore	Ground
Lemur catta	0.1 (19)	NA	NA	NA	NA	NA	NA	NA	0.87 (93)	NA	NA	NA	NA	NA	NA	NA
Papio cynocephalus	0.08 (21)	19 (21)	Absent (29)	Present (50)	Absent (60)	Absent (60)	1.42 (78)	Present (106)	NA	Present (81)	1.00	156.10	116.00	NA	Carnivore	Ground
Pygathrix roxellana	0.075 (22)	3 (22)	Absent (32)	Absent (51)	Absent (60)	Absent (60)	NA	Present (51)	0.66 (96)	Present (81)	1.00	NA	NA	14750.00	NA	Arboreal

Elephas maximus	0.07 (1)	7 (1)	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (107)	NA	Present (84)	1.00	5084.35	NA	3178000.00	Herbivore	Ground
Gorilla beringei	0.07 (1)	4 (1)	Absent (114)	Absent (40)	Absent (60)	Absent (60)	1.16 (73)	Present (115)	NA	Absent (115)	0.67	NA	NA	NA	NA	NA
Cervus elaphus	0.06 (24)	4 (24)	Absent (29)	Absent (52)	Absent (60)	Absent (60)	0.78 (79)	Present (52)	NA	NA	1.00	335.90	218.78	165111.00	Herbivore	Ground
Gorilla gorilla	0.06 (1)	4 (1)	Absent (1)	Absent (53)	Absent (60)	Absent (60)	NA	Present (53)	NA	Absent (81)	0.50	470.26	341.44	120614.00	Herbivore	Ground
Aepyceros melampus	0.03 (26)	NA	NA	NA	NA	NA	NA	NA	0.88 (98)	NA	NA	NA	NA	NA	NA	NA
Equus caballus	0.03 (25)	3 (25)	Absent (33)	Absent (48)	Absent (60)	Absent (60)	NA	Present (97)	0.9 (97)	Present (84)	1.00	642.74	NA	246073.00	NA	Ground
Vicugna vicugna	0.02 (1)	NA	Absent (1)	NA	Absent (60)	Absent (60)	NA	Present (108)	NA	NA	1.00	199.90	NA	50000.00	Herbivore	Ground
Ateles belzebuth	0.01 (1)	NA	Absent (1)	Absent (57)	Absent (60)	Absent (60)	NA	Present (117)	NA	NA	1.00	112.70	48.88	6467.00	Herbivore	Arboreal
Oreamnos americanus	0.01 (28)	6 (28)	NA	NA	NA	NA	1.79 (79)	NA	NA	NA	NA	NA	NA	NA	NA	NA
Pan troglodytes	0.01 (1)	12 (1)	Absent (1)	Present (58)	Absent (60)	Absent (60)	NA	Present (109)	0.71 (93)	Present (81)	1.00	375.98	291.59	41301.00	Herbivore	Ground
Pan paniscus	0 (1)	9 (1)	Absent (1)	Absent (59)	Absent (60)	Absent (60)	NA	Present (110)	0.61 (93)	Present (81)	1.00	328.00	242.36	36329.00	Herbivore	Ground

749

750 **Supporting References**

751

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753 allomaternal care are positively correlated and conserved throughout the mammalian
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Supplementary Table S2: Results from regressions of ecological parameters on the rate of aggression among female group members

Herbivore vs Carnivore vs Omnivore: n=22 species, all p>0.63

Lifespan: n=13 species, p=0.94

Environmental Harshness: n=13 species, p=0.98

Arboreal vs Ground: n=22 species, all p>0.84

Seasonal breeding: n=17 species, p=0.79

Supplementary Table S3: Results from regressions of brain mass on the expression of traits associated with relational complexity. All analyses include the phylogenetic relatedness among the 43 species (26 species in the analysis including rainfall seasonality and diet) as a covariate.

BrainMass_g ~ RelationalComplexity

	post.mean	l-95% CI	u-95% CI	pMCMC
(Intercept)	3.348	2.522	4.197	< 8e-05 ***
RelationalComplexity	1.842	0.698	2.904	0.00078 ***

BrainMass_g ~ BodyMass_g + RelationalComplexity

	post.mean	l-95% CI	u-95% CI	pMCMC
(Intercept)	-2.3542	-2.9905	-1.7260	< 8e-05 ***
RelationalComplexity	0.4560	0.1105	0.7921	0.00961 **
BodyMass_g	0.6811	0.6107	0.7509	< 8e-05 ***

BrainMass_g ~ BodyMass_g + RelationalComplexity + Diet

	post.mean	l-95% CI	u-95% CI	pMCMC
(Intercept)	-2.57177	-3.32084	-1.82613	< 8e-05 ***
RelationalComplexity	0.52710	0.17328	0.86694	0.00472 **
BodyMass_g	0.69429	0.62212	0.76397	< 8e-05 ***
DietHerbivore	-0.03875	-0.42158	0.34620	0.83260
DietOmnivore	0.33121	-0.08629	0.76995	0.12079

BrainMass_g ~ BodyMass_g + RelationalComplexity + Arboreality

	post.mean	l-95% CI	u-95% CI	pMCMC
(Intercept)	-2.32499	-2.91525	-1.69945	<8e-05 ***
RelationalComplexity	0.40730	0.06860	0.74700	0.0203 *
BodyMass_g	0.70539	0.63161	0.78137	<8e-05 ***
StrataGround	-0.31431	-0.69025	0.07247	0.100

NeocortexMass_g ~ RelationalComplexity

	post.mean	l-95% CI	u-95% CI	pMCMC
(Intercept)	2.223	0.621	3.801	0.0117 *
RelationalComplexity	2.957	1.062	5.076	0.0052 **